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FORM AND FUNCTION OF THE ASYMMETRIC CHELAE IN BLUE CRABS WITH NORMAL AND REVERSED HANDEDNESS

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Abstract

The form and function of the paired asymmetric chelae were examined in blue crabs with the normal (right crusher, left cutter) and reverse (left crusher, right cutter) chela laterality or handedness. The force generated by the crusher chela in intact blue crabs was significantly greater than that of its counterpart cutter chela. The relative strength of the crusher is due to its greater mechanical advantage and larger muscle volume. The closer muscles of both chelae were capable of exerting similar forces. For a comparable frequency of stimulation, the fast excitor axon was more effective in the cutter than in the crusher chela. The paired closer muscles were composed of fibers with long sarcomere lengths (>6 μm) characteristic of slow fibers with no significant difference in their mean value or in their distribution between crusher and cutter chelae. This was corroborated by finding that the myofibrillar ATPase activity and oxidative capacity was uniformly similar over most of the muscle in both chelae except for some differentiation in the most proximal and distal regions of the muscle. Such homogeneity in sarcomere lengths and enzymatic properties of the paired closer muscle occurred in blue crabs with the normal and reverse chela laterality. Thus functional differences brought about by motoneuron activation between the asymmetric chelae are probably due to muscle fiber properties other than their sarcomere lengths and enzymatic profiles, such as their cable and contractile properties as well as to neuronal and neuromuscular properties.

Introduction

A prominent feature of many crustaceans is the bilateral asymmetry of the paired chelae consisting of a major (crusher) chela which is usually larger and more elaborate in form than the minor (cutter) chela. Striking examples of such chela dimorphism are found among male fiddler crabs, snapping shrimp, and lobsters, in all of which the paired chelae behave differently as well. In the male fiddler crab *Uca,* the major chela is used for territorial defense and courtship display while the minor is used for feeding and grooming (Crane, 1975). Similarly in the snapping shrimp, *Alpheus,* the major chela functions in agonistic behavior and the minor in manipulating objects. In the lobster *Homarus,* the crusher chela, which is slow-acting and powerful, is used for crushing the shells of mussels, etc. (Herrick, 1895), and the cutter chela, which is fast-acting but weaker, has been observed to capture swimming fish (Lang *et al.,* 1978). The basis for these different behaviors in the lobster *Homarus americanus* has been attributed to chela morphology including the fiber composition of the closer muscle. Crusher chelae have greater mechanical advantage and closer muscle volume than similarly sized cutter chelae (Elner and

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Campbell, 1981). The crusher closer muscle is composed of all slow fibers while the cutter closer muscle has a majority of fast fibers and few slow fibers (Jahromi and Atwood, 1971; Lang *et al.*, 1977; Ogonowski *et al.*, 1980).

The blue crab, *Callinectes sapidus* Rathbun, also has dimorphic crusher and cutter chelae which have different functions in feeding. The crusher, which is capable of generating much more force than the cutter, is used in crushing mollusc prey, while the cutter manipulates the prey item and tears at the exposed flesh (Blundon and Kennedy, 1982). However, there is little available data on the functional and structural differentiation of the dimorphic chelae or on the composition of their closer muscles. The present study addressed these points.

Another reason for studying blue crabs is the apparent reversal of chela laterality that they display. The normal chela laterality is right crusher and left cutter (Przibram, 1931). However, the reverse configuration of left crusher and right cutter which occurs in a small percentage (14.4%) of the population and among large crabs only, suggested to Hamilton *et al.* (1976) that this configuration could arise when the crusher is lost and in its place a cutter regenerates. The existing intact cutter transforms into a crusher. Reversal of chela laterality found in the snapping shrimp *Alpheus*, involves a transformation in the fiber composition of the closer muscles (Stephens and Mellon, 1979; Mellon and Stephens, 1980). It was therefore of interest to determine the fiber composition of the closer muscle in blue crabs with the normal and reversed chela laterality.

Materials and Methods

Chela performance in vivo

Blue crabs weighing between 150 g and 260 g were caught with crab pots in the Choptank River, Chesapeake Bay, in June 1984. They were placed in water tables (at Horn Point Environmental Laboratory, Cambridge, Maryland) supplied with running estaurine water (25°C) for 24 hours before testing. Crabs were induced to grip two steel bars of a force transducer (Fig. 1). One bar was connected to a

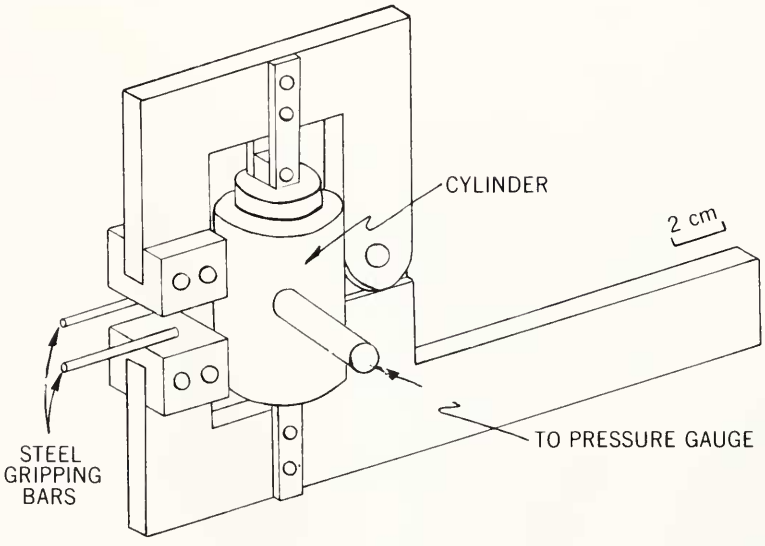

Figure 1. Diagram of the force transducer used to measure the force exerted by the chelae in intact blue crabs. Scale mark = 2 cm.

stainless steel cylinder, the other bar was attached to a piston which inserted into the cylinder. The cylinder was filled with vacuum pump oil. Squeezing the bars together raised the pressure inside the cylinder which was shown on a pressure gauge. The transducer was calibrated by hanging a weight on the proximal and distal ends of the steel bars and recording the deflection on the pressure gauge. Force recordings were taken from both crusher and cutter chelae of the crabs. The points of force application along the bars of the transducer and along the dactyls were measured with dial calipers. The force applied to the transducer by the dactyl (F_{bar}) was used to calculate the force applied by the closer muscle to the dactyl at the point of apodeme insertion (F_1). Assuming the dactyl pivot is frictionless, then

$$F_1 = (F_{bar})(L_{bar})/L_1$$

where L_1 is the distance from the dactyl pivot to the point of apodeme insertion onto the dactyl, and L_{bar} is the distance from the dactyl pivot to the point of force application along the dactyl (Fig. 2). The product of (F_1) (L_1) divided by the distance from the dactyl pivot to any point x along the dactyl equals the dactyl force at point x. Other measurements included carapace width, chela length, chela height, chela thickness, mechanical advantage (L_1 divided by the distance from the dactyl pivot to the dactyl tip), angle of muscle fiber pinnation, and surface area of both sides of the apodeme. After removing the dorsal surface of the propodus and the chela opener muscle, the dactyl was fixed open at 30° (to simulate its crushing position) and viewed under a dissecting microscope equipped with a camera lucida drawing tube. The apodeme and several muscle fibers on both sides of the apodeme were traced; the angles of muscle fiber attachment onto the apodeme (angles of pinnation) were then measured with a protractor. The apodeme was subsequently

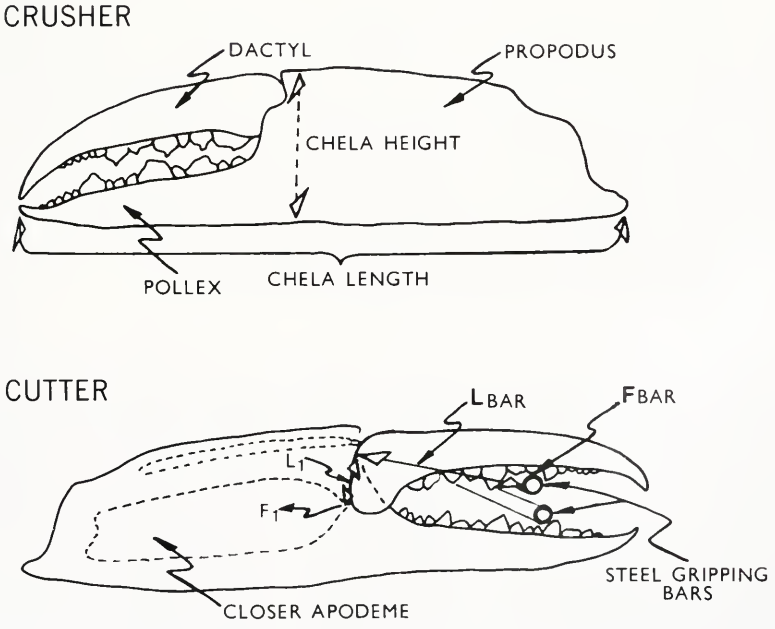

FIGURE 2. Crusher and cutter chelae of *Callinectes sapidus* showing the mechanical and morphological parameters used to characterize the chelae.

dissected away from the chela. Its area was measured with a meter conventionally used by botanists to measure leaf surface area.

The amount of stress (S) per unit of muscle fiber cross-sectional area was determined by

$$S = F_1/A \sin 2\theta$$

where F_1 is the force applied to the dactyl by the closer muscle, A is the area of one side of the apodeme (the formula uses total apodeme area 2A) and θ is the mean angle of pinnation (Alexander, 1969).

The means of all strength and morphological measurements were compared among right and left crushers and cutters using a one-way analysis of variance. If this test rejected the null hypothesis that the measurements were similar, a Student-Newman-Keuls multiple comparison test was then used to determine which means were significantly different ($\alpha = 0.05$) (Sokal and Rohlf, 1969).

Chela performance in situ

Callinectes sapidus weighing between 150 and 180 g were purchased from local suppliers and held in artificial sea water (at University of Toronto, Scarborough, Ontario) at approximately 10°C for a few days before being used. All experiments were performed on crabs with fully differentiated crusher and cutter chelae and not on regenerating chelae which were recognized by their relatively smaller size. The majority of animals used had right crusher and left cutter chelae while a few had the opposite configuration of right cutter and left crusher and even fewer had both chelae of the cutter type. We have not as yet encountered any blue crabs with paired crusher chelae.

In order to determine the closing behavior of a chela, it was removed from the animal by inducing autotomy. Next the nerve to the chela closer muscle was exposed in the carpus where it was stimulated via platinum wire electrodes. The resulting axon spike was recorded extracellularly via a suction electrode placed more distal to the point of stimulation. The preparation was bathed in 10°C marine saline (470 m*M* NaCl, 8 m*M* KCl, 10 m*M* $MgCl_2$, 15 m*M* $CaCl_2$, 33 m*M* glucose, 10 m*M* HEPES at pH 7.4). The fast and slow axons in the closer nerve were selectively stimulated with 0.1 ms pulses either by varying the stimulus intensity or the placement of the nerve on the electrodes. Resulting contractions of the dactyl were monitored by having its distal end attached to a probe fitted to the moveable anode pin of an RCA 5734 mechano-electric transducer.

Muscle composition

The fiber composition of the closer muscle was assessed in two ways: by measuring the average sarcomere length (SL) of histologically fixed fibers or by staining for myofibrillar ATPase and NADH dehydrogenase activity in frozen cross sections of the muscle. In the former method, the closer muscle was exposed on its dorsal surface by removing the overlying opener muscle and injected with alcoholic Bouins fixative in which it was allowed to saturate for 24 h (Lang *et al.*, 1977). Care was taken to ensure that the fibers were fixed in a relaxed position by holding the dactyl partly open. Subsequently, the closer muscle was exposed and divided into nine sections along its inner face in order to sample all areas (Lang *et al.*, 1977). The samples were then stored in 75% ethanol. Measurements of SL were made in teased wet mount preparations using a compound microscope equipped

with a micrometer. Five consecutive sarcomeres were measured at 3 separate regions of a myofibril and this total of 15 sarcomeres gave an average SL for a fiber. Usually 10 fibers were measured in each of the 9 samples, for a total of 90 fibers for each muscle. Three pairs of closer muscles were analyzed with the above technique for the normal chela laterality of right crusher and left cutter; one pair for the reverse configuration of right cutter and left crusher and one pair for the paired cutter configuration.

For the histochemical study, the cuticle of the chela was ground down to almost the hypodermis with a high speed hobby drill. The entire propodus was mounted on a chuck, coated with embedding material and frozen in isopentane chilled with liquid nitrogen. Serial thick (16 μm) cross-sections were obtained by methods described elsewhere (Ogonowski and Lang, 1979). Histochemical techniques for detecting myofibrillar ATPase activity were modified from a method by Padykula and Herman (1955) and these modifications are described elsewhere (Tse *et al.*, 1983). Staining methods for NADH dehydrogenase was first described by Nachlas *et al.* (1958). Four pairs of chelae were analyzed histochemically for crabs with the normal laterality of right crusher and left cutter; two pairs for the reversed configuration of left crusher and right cutter, and one pair for the paired cutter configuration.

Results

Chela performance in vivo

In blue crabs with the normal laterality of right crusher and left cutter the dactyl of right crushers exerts greater force than the dactyl of left cutters (Table I). However, there was no significant difference in stress exerted by crusher or cutter

Table I

Mechanical and morphological measurements (mean ± SD) of the paired crusher and cutter chela of blue crabs, Callinectes sapidus

	Normal laterality		Reversed laterality	
	Right crusher (n = 18)	Left cutter (n = 18)	Left crusher (n = 9)	Right cutter (n = 9)
Force at dactyl tip (newtons)	42.8 ± 13.8^{a}	24.6 ± 7.3^{b}	31.2 ± 8.9^{b}	19.9 ± 8.0^{b}
Muscle stress (newtons/cm^2)	63.8 ± 17.8^{a}	51.4 ± 14.3^{ab}	60.2 ± 18.8^{ab}	45.2 ± 12.1^{b}
Mechanical advantage	0.216 ± 0.012^{a}	0.171 ± 0.016^{b}	0.188 ± 0.011^{c}	0.176 ± 0.011^{bc}
Apodeme area/ chela length	0.0429 ± 0.0044^{a}	0.0374 ± 0.0035^{bc}	0.0397 ± 0.0057^{ab}	0.0344 ± 0.0057^{c}
Chela height/ chela length	0.273 ± 0.012^{a}	0.253 ± 0.010^{b}	0.263 ± 0.006^{c}	0.252 ± 0.012^{b}
Chela thickness/ chela length	0.221 ± 0.011^{a}	0.211 ± 0.011^{b}	0.218 ± 0.008^{ab}	0.207 ± 0.009^{b}
Chela length/ carapace width	0.543 ± 0.019^{a}	0.542 ± 0.019^{a}	0.539 ± 0.021^{a}	0.534 ± 0.026^{a}

Means with at least one superscript letter in common are not statistically different (α = 0.05).
Apodeme area measured in cm^2; chela height, length, and thickness measured in mm.

closer muscles. Right crushers possessed a significantly greater mechanical advantage, apodeme size, chela height, and chela thickness, than their counterpart left cutters. The chela length, however, was similar between the dimorphic claws.

Angles of pinnation along the distal-proximal axis of the dorsal surface of the crusher and cutter closer muscles were similar except for the most proximal 10% of the muscle, where the angles became more acute. A similar pattern of fiber arrangement has been found in the shore crab *Carcinus maenas* (Warner *et al.*, 1982). Mean angles of pinnation between right and left crushers and between right and left cutters were not significantly different, although cutters had a significantly greater angle of pinnation than crushers (33° and 31° respectively). Angles of pinnation were not measured for fibers deeper within the muscle, although Warner *et al.* (1982) found such fibers of *C. maenas* to have similar angles relative to the dorsal fibers.

In animals with the reversed laterality of left crusher and right cutter, the crushers were not able to exert greater forces than the cutters (Table I). Left crushers had greater apodeme size and chela height than right cutters, but had similar values of mechanical advantage, chela thickness, and chela length. When comparing similarly sized right and left crushers from two different crabs, left crushers were weaker and had a smaller mechanical advantage.

These measurements were taken from male crabs. A few measurements from female crabs revealed differences between the dimorphic chelae which were similar to those for the male. However, female crusher and cutter chelae were approximately 30% and 23% shorter than their male counterparts for crabs with similar carapace widths.

Chelae performance in situ

The fast axon to the chela closer muscle was readily distinguished from the slow axon because it usually had a lower threshold for firing and a higher conduction velocity. Both these features are shown in the extracellular recording of their spikes from the closer nerve (Fig. 3A). It was therefore possible by the appropriate placement of the electrodes to fire each axon by itself and to record the closing behavior it evoked.

In the cutter chela (Fig. 3B) stimulation of the fast axon at 1 Hz evoked small twitches only when twin pulses (6–8 ms apart) were used. The individual twitches were visible after a couple of stimuli and they summated markedly with each succeeding stimuli thereafter. At a higher frequency of contraction such as 20 Hz, a smooth contraction resulted which increased in speed as the frequency was raised. Stimulation of the slow axon to this same muscle evoked a barely perceptible contraction which increased in speed and strength as the frequency was increased.

In the crusher chela (Fig. 3C) no twitch contractions were seen even with twin pulses at 5 Hz at which frequency, however, a small tonic contraction was evident. Increasing the stimulating frequency to 20 Hz dramatically increased the closing behavior of the chela. The slow axon to this muscle evoked a small contraction at about 50 Hz stimulation. Doubling the rate of stimulation correspondingly increased the speed of chela closing.

The above results highlight two important points concerning chela closing behavior in blue crabs *viz.* (1) that within each chela the fast axon is effective at a much lower frequency of firing than the slow axon and, (2) that the axons to the cutter chela are effective at a lower frequency of firing than their homologs in the crusher chela.

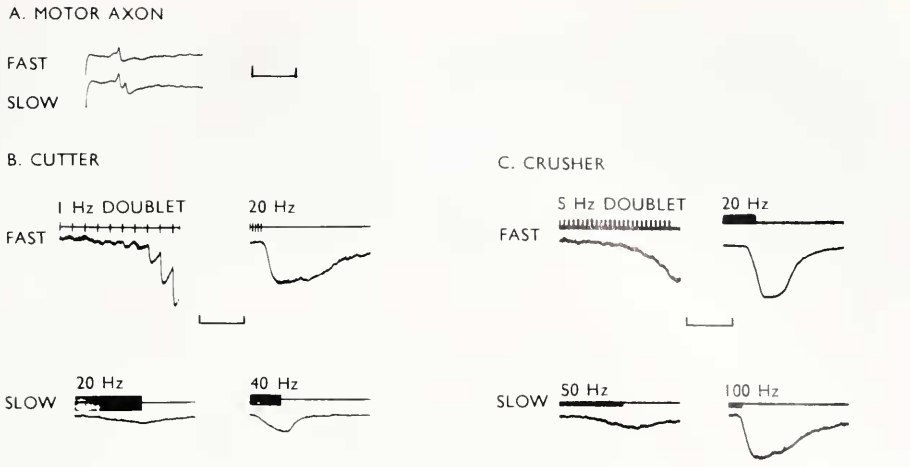

FIGURE 3. A. Extracellular recording from the closer nerve to the crusher chela showing a fast axon spike by itself (upper trace) which is followed at a higher stimulating voltage by a slow axon spike which has a slower conduction velocity (lower trace). B, C. Closing behavior of the paired cutter and crusher chelae with stimulation of fast and slow axons to the closer muscle. The upper trace monitors the stimuli and the lower trace records the closing movement of the dactyl. Calibration: A, 5 ms, B, fast contractions 0.2 s; slow contractions 0.5 s; C, fast contractions 0.5 s; slow contractions 0.2 s.

Muscle composition

The fiber composition of the paired cutter and crusher muscles based on sarcomere length (SL) was essentially similar (Fig. 4). Both have fibers with only long (>6 μm) SL which are typical of slow fibers. The range of SL extended between 6 to 15 μm in all five blue crabs examined. The mean SL calculated for each

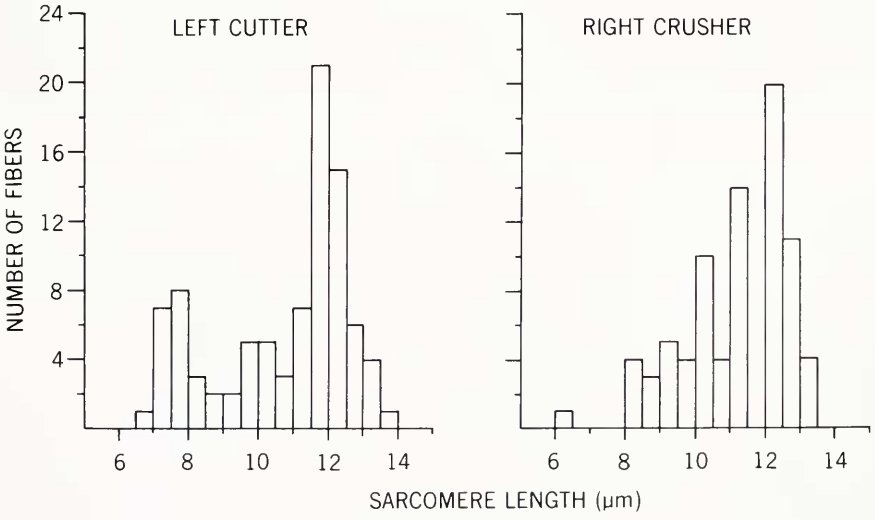

FIGURE 4. Frequency histogram of muscle fibers with characteristic sarcomere lengths from paired closer muscles of a blue crab with the chela laterality of right crusher and left cutter. Ninety fibers were sampled in each muscle.

chela was not significantly different from that of its counterpart (Table II). Furthermore, muscle fiber populations were compared using the Kolmogorov-Smirnoff two-sample test and showed no significant differences in all five blue crabs listed in Table II. These results demonstrate that the paired chela closer muscles are essentially similar in their fiber composition (consisting of all slow fibers) in any three of the chela configurations examined in this study.

The paired closer muscles were also examined by cutting cross-sections of the entire chelae and staining for myofibrillar ATPase and NADH diaphorase activity in several animals. In both claws the muscles stained with a uniform intensity over most of its length (Fig. 5B, F) suggesting a uniform population of fiber types in keeping with the SL measurements. However, some differentiation within this slow fiber population was seen especially in the proximal and distal regions of the muscle. In the distal region a small group of central fibers close to the exoskeleton showed a lower ATPase and higher diaphorase activity than the remaining fibers (Fig. 5A, E). In the proximal region, a central band of fibers extending between apodeme and exoskeleton displayed a much higher ATPase and diaphorase activity than the remainder (Fig. 5C, G). In some cases this proximal region was even further differentiated showing at least three intensities of staining for ATPase activity (Fig. 5D).

Discussion

The fiber composition of the closer muscle in the paired crusher and cutter chelae is similar, consisting of all long SL (>6 μm), slow fibers. Within this category of slow fibers there is some further differentiation into subtypes especially in the proximal region of the muscle where several intensities of myofibrillar ATPase staining were seen. Such differentiation within slow fibers has been seen in lobster muscle as well (Kent and Govind, 1981; Costello and Govind, 1983), and underscores the fact that there may well be a continuum of sub-types within the broad category of slow muscle. The paired muscles are also similar in the amount of stress they exert per unit cross-sectional area. Despite these similarities there are some functional differences between the asymmetric chelipeds in their closing behavior. Thus the force during claw closure developed *in vivo* was significantly greater for the crusher than the cutter claw. This is attributable in part to the larger muscle volume and

Table II

Mean sarcomere length (μm) of paired chela closer muscles from Callinectes sapidus *with various chela lateralities*

		Left cutter		Right crusher		
	Body wt (g)	Mean ± SD		Mean ± SD		*P*
#1	170	10.51 ± 1.38	90	10.97 ± 0.47	90	ns
#2	161	10.61 ± 1.23	90	11.52 ± 0.82	90	ns
#3	142	10.42 ± 1.67	60	11.17 ± 0.89	60	ns
		Left crusher		Right cutter		
#4	137	10.51 ± 1.29	90	10.42 ± 2.05	90	ns
		Left cutter		Right cutter		
#5	154	12.13 ± 1.53	90	11.66 ± 1.53	90	ns

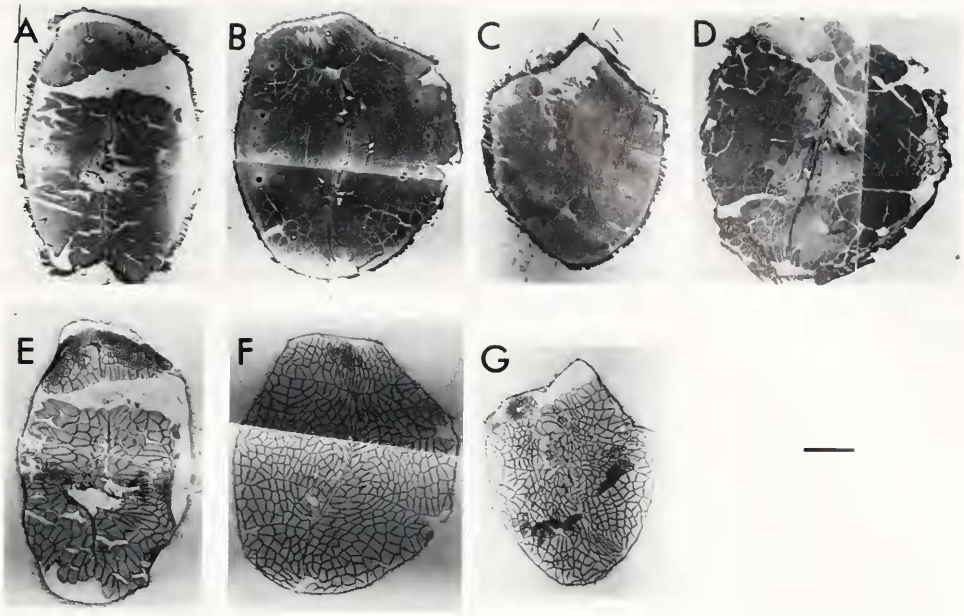

FIGURE 5. Frozen cross-sections taken through the distal (A, E), middle (B, F) and proximal (C, D, G) regions of a crusher chela and stained for myofibrillar ATPase (upper row) and NADH diaphorase (lower row) activity. The closer muscle occupies most of the cross-sectional area of the propodus with the opener muscle occupying a small area in the dorsal part of the chela. Adjacent sections for ATPase and NADH diaphorase are shown for each region from one chela and a single proximal section (D) from another crusher chela is shown to emphasize the variation in ATPase activity in this region. Scale mark = 1 mm.

greater mechanical advantage of the crusher compared to the cutter and it may also be attributable to motor firing patterns. In the latter respect the experiments on isolated chelae showed clear differences between cutter and crusher types. The cutter chela gives twitch contractions to twin pulses whereas the crusher does not twitch. Presumably some of the slow fibers in the cutter closer muscle are of the fast-follower type in their contractile characteristics as has been demonstrated among slow fibers in the lobster closer muscle by Jahromi and Atwood (1971) and more recently by Costello and Govind (1983). These fast-follower types have relatively short rise times when depolarized and this would account for the twitch-type contraction. The crusher closer muscle in the blue crab judging from its inability to twitch, would presumably have no fast-follower types among its slow fibers. Further functional differentiation between cutter and crusher chelae in blue crabs is seen in the fact that for a comparable stimulus frequency the cutter closer muscle contracts more effectively than its crusher counterpart. This taken together with the finding that the crusher chela generates greater force than the cutter would make the paired chelae suited to perform different roles in feeding if not in other behaviors as well.

Chela asymmetry in the blue crab, when compared with other crustaceans in which asymmetry has been studied, shows the least degree of specialization. The present study uncovered a functional and structural asymmetry between major and minor chelae in blue crabs with no corresponding asymmetry in the composition or strength of the closer muscles. Furthermore we would predict that there are no asymmetries in the size of motoneurons or the number of sensory axons to the

chelae based on the fact that they are not greatly different in size. A somewhat greater degree of specialization between the paired chelae is seen in the lobster *Homarus americanus*. Not only do the lobster chelae show functional asymmetry (Govind and Lang, 1974) but there is also a corresponding asymmetry in the fiber composition of the paired closer muscles (reviewed by Govind, 1981). Forces measured at the dactyl of lobster chelae can be five to ten times greater in the crusher than the cutter. The crusher has greater mechanical advantage and muscle volume than the cutter, but even after these differences have been taken into consideration, the crusher closer muscle exerts two to three times the stress displayed by the cutter chelae (Blundon, unpub.). There is, however, no asymmetry between homologous motoneurons to the closer muscle (Hill and Govind, 1983) nor in the size or number of sensory axons to the paired chelae (Govind and Pearce, 1985). The greatest degree of specialization between the paired chelae occurs in the snapping shrimp *Alpheus* (reviewed by Mellon, 1981). In this genus, the functional asymmetry (Przibram, 1931; Wilson, 1903) is complemented by asymmetries in the fiber composition of the closer muscle (Stephens and Mellon, 1979; Mellon and Stephens, 1980) in the size of the motoneuron somata to the closer muscle (Mellon *et al.*, 1981), and in the number of sensory axons to the chelae (Govind and Pearce, 1985).

Finally, with regard to the reversal of chela asymmetry proposed by Hamilton *et al.* (1976) for blue crabs, the present report shows that such reversal would not involve changes in the sarcomere length, myosin ATPase activity, or oxidative capacity of the closer muscles. They may, however, involve changeover of the contractile properties from fast-follower type fibers to slow-follower type in the transforming cutter-to-crusher chela. They certainly involve changes in the external form of the chela; the cutter acquires a heavier dentition and possibly a slightly larger muscle in its transformation into a crusher. The mechanical advantage and muscle volume of the newly formed left crusher, although being superior to the newly regenerated right cutter, is not as great as the original crusher. More importantly, the essential similarity in SL and enzyme properties between the closer muscle of the cutter and crusher claws demonstrates that these muscle properties are not responsible for any functional differences between the paired claws brought about by firing of their motoneurons. Rather these differences are in part due to properties of their motor axons, such as conduction velocities, and their neuromuscular synapses, such as the amount of transmitter released and the degree of facilitation. Part of the functional differentiation may also be due to properties of the muscle fibers themselves such as differences in cable properties and in the threshold for excitation-contraction coupling.

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